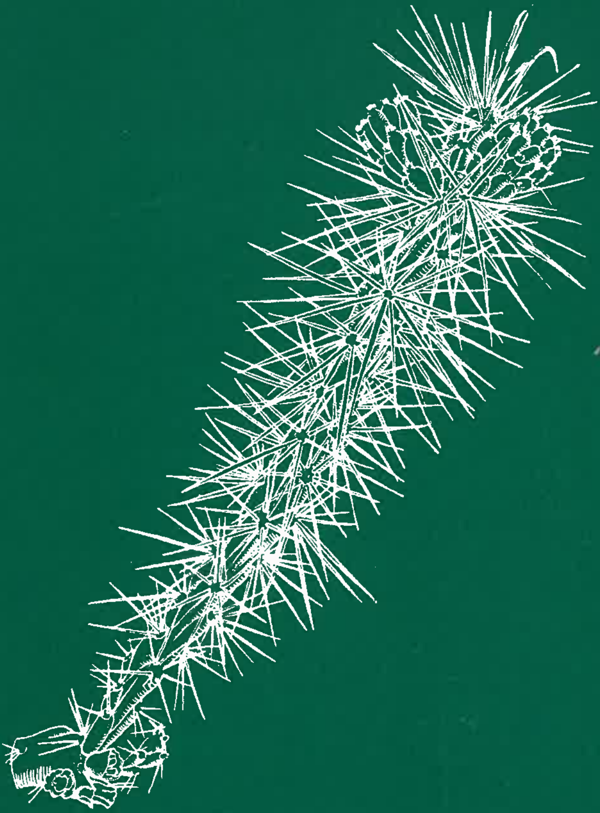


Mr. Carnegie's Plant Biologists

About the Carnegie Institution

Andrew Carnegie in January 1902 founded and endowed the Carnegie Institution of Washington, to encourage "investigation, research, and discovery, and the application of knowledge to the improvement of mankind." Today, ninety years later, Mr. Carnegie's "institution for discovery" continues to operate five research centers—the Department of Embryology in Baltimore, Maryland, the Department of Plant Biology at Stanford, California, the Geophysical Laboratory and the Department of Terrestrial Magnetism, both in Washington, D.C., and the Observatories of the Carnegie Institution, in Pasadena, California and Las Campanas, Chile.

The Institution is led by its president, Maxine Singer. Her predecessors, most of whom played significant roles in the history offered here, were:

Daniel Coit Gilman, 1902–1904
Robert S. Woodward, 1904–1920
John C. Merriam, 1921–1938
Vannevar Bush, 1939–1955
Caryl P. Haskins, 1956–1971
Philip H. Abelson, 1971–1978
James D. Ebert, 1978–1987

The Department of Plant Biology is led by its director, Winslow Briggs, whose appointment in 1973 concludes this essay. The previous leaders of the Carnegie plant biologists were:

Daniel T. MacDougal, 1904–1928
Herman A. Spoehr, 1929–1930, 1931–1947
C. Stacy French, 1947–1973

Cover drawing: Joint of *Opuntia whipplei.* This low-standing, heavily branched member of the cactus family is distributed over the southwestern United States. Drawn here about half-size, from N. L. Britton and J. N. Rose, *The Cactaceae: Descriptions and Illustrations of the Cactus Family,* I:55, Carnegie Institution of Washington publication 249 (1919).

Mr. Carnegie's Plant Biologists:

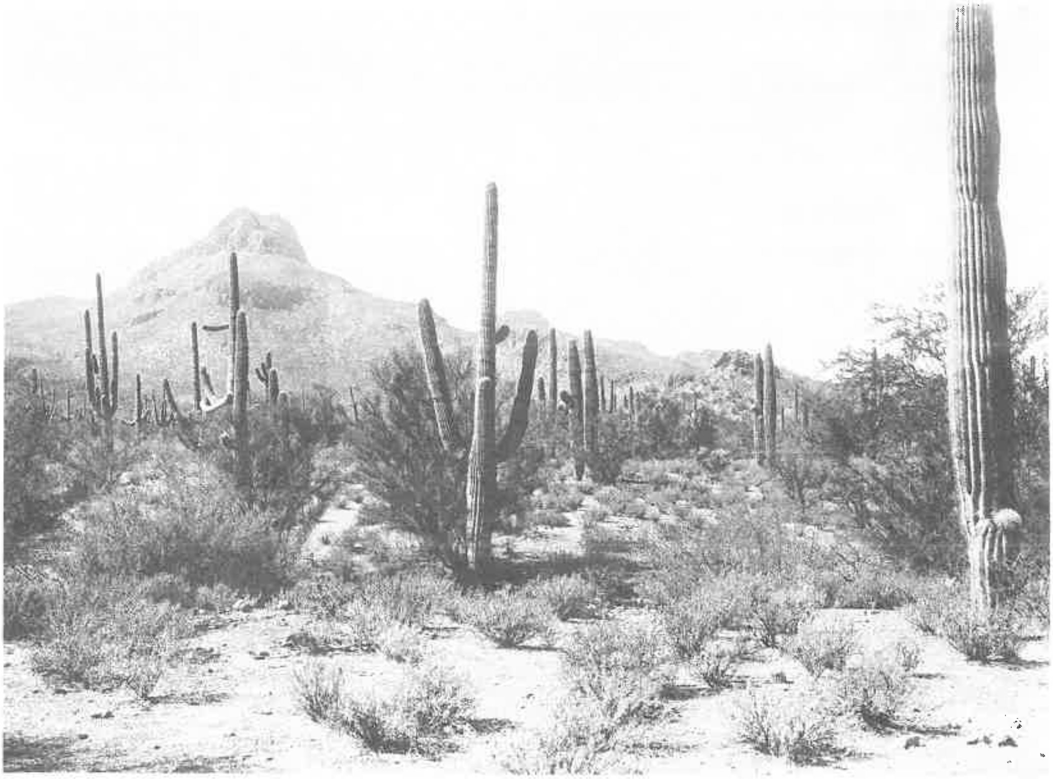
The ancestry of Carnegie Institution's DPB

1902

by Ray Bowers

with the advice and encouragement of Winslow Briggs

Carnegie Institution of Washington
1992



Desert plant life, 16 miles northwest of the Desert Laboratory, c. 1930.

Part I. To 1928

By the year 1902, plant scientists everywhere had come to accept the idea of evolution in nature. There was little agreement, however, as to how, and to what extent, natural selection worked. The gene was known only as a vague idea (the word was not yet in use), and chromosomes were not yet acknowledged to be the bearers of the hereditary blueprint. Plant breeding was widely practiced, often through the asexual cloning of individuals by cuttings or grafts or through artificial pollination. Mendel's earlier discoveries, unknown to breeders and scientists for decades but now being rediscovered by European scientists, offered intriguing clues to the workings of heredity. In the United States, investigators at the agricultural research stations carried on applied research on crop plants, while a few scientists at universities and botanical gardens pursued research for basic understanding.

Many plant biologists invested much effort into classifying plants by interpreting varied evolutionary, morphological, and physiological evidence. The physiology, or functioning, of higher plants was understood for the most part only broadly, and the chemistry of photosynthesis was unknown except in speculative and often incorrect theory. The comment was occasionally heard that plant biology, as well as other realms of biology, should move away from the domain of the naturalist and become more quantitatively and experimentally oriented, i.e., like physics and chemistry.

In highly formative stage was a relatively new branch of study, called plant ecology, which dealt with the mutual relations of plants and their environments. Plant ecology was seen to encompass two broad topics—the reactions of the *individual plant* and its components to its environment ("physiological ecology"), and the development of *plant communities* and their habitats.

The Origins of the Desert Laboratory

The Carnegie Institution's decision in its first year to create a desert botanical laboratory reflected both the scientific merits of the idea as well as several favorable occurrences of personality and outlook.

It was propitious, for example, that the Institution's advisory committee on botany, formed in March 1902, included Nathaniel L. Britton, director of the New York Botanical Garden. Britton was an acquaintance of Andrew Carnegie, who, interested in plant life, had been vice president of the Garden's Board. Britton would remain a valued advisor in Carnegie affairs for many years, and would later co-author a classic four-volume study of cactus, published by Carnegie Institution.

The chairman of the advisory committee

The original building, completed in 1903, at the Desert Laboratory.

was Frederick V. Coville, a prominent scientist of the U. S. Department of Agriculture, known for his interest in the adaptations and habitats of plants in desert regions. Coville proposed to the committee his long-cherished idea for a laboratory in the southwestern United States for "the study of the life history of plants under desert conditions," with special attention to the absorption, storage, and transpiration of water. There were several botanical laboratories in temperate and tropical humid regions, he wrote, but "a desert botanical laboratory exists nowhere in the world." Coville noted the economic advantages of such a laboratory, predicting that the nation's arid regions would experience enormous development of population, industry, and agriculture in the next century. The agricultural experiment stations in the arid states, he wrote, were simply unequipped to undertake the needed investigations into "fundamental processes of plant growth."

Coville's plan became one of several recommendations in the advisory committee's final report, June 28, 1902. Later in the year, Coville became "confidential advisor in botany" to the Institution's executive committee, and soon afterwards, on November 25, 1902, the Carnegie Board of Trustees voted funds to establish and maintain a Desert Botanical Laboratory. A two-man advisory board was established to "supervise and direct" the venture. The board members were Coville and the director of laboratories at the New York Botanical Garden, Daniel Trembly MacDougal (1865–1958). In late January 1903, Coville and MacDougal began a several-week exploration of the Southwest, traveling by rail, road, and horseback in search of a future site for the laboratory.

The traveling board members evaluated matters of climate and flora, accessibility, and habitability. Their verdict was unproblematic. Tucson was a lively town of 10,000, located on the transcontinental railroad, and home to the University of Arizona and the Arizona Agricultural Experiment Station. Tucson's climate and vegetation were unmistakably arid, and the surrounding regions offered a variety of desert lands. The local Chamber of Commerce offered title to 40 acres on uninhabited Tumamoc Hill, just west of the town, along with provision for water, electricity, and a roadway.

Things happened fast in those supposedly slower times. On March 18, 1903, the Carnegie executive committee accepted the Chamber's offer and authorized initial construction at the Tumamoc site.

Early Days at the Desert Laboratory

Though Coville and MacDougal visited occasionally, daily affairs at the Desert Laboratory were managed by the resident investigator, William A. Cannon (1870-1958), recently of the New York Botanical Garden. A one-story laboratory building was completed in 1903, furniture and equipment were procured, and research programs quickly emerged.

Cannon himself began studies of water absorption and storage in the roots of desert plants, and worked on a new apparatus for measuring water transpiration. Established investigators, including Volney Spalding, Burton E. Livingston, and F. E. Lloyd, visited from their home universities for varied studies of desert plants, supported by grants from Carnegie Institution. Cannon in June 1904 wrote of the sizzling heat and wondered how the expected summer visitors, Livingston and Lloyd, would fare. (Both men thrived, and both would later become full-time staff members).

Meanwhile, the trustees of the Carnegie Institution were rapidly shaping the Institution's future by starting several new departments and other major grant programs. Much of the energy stemmed from the executive committee, led by John S. Billings, but Billings's vigor led to conflicts over roles with the Institution's elderly president, Daniel Coit Gilman (1831–1908). Gilman's resignation over the subordination of the presidency was accepted by the Board in December 1904; Gilman's successor, Robert S. Woodward (1849–1924), thus faced the large challenge not only to continue shaping the still-infant Institution but also to establish his own leadership in the process.

Woodward moved strongly following his summer 1905 visit to the Desert Laboratory, where he found "no competent head." Meeting privately with Daniel MacDougal, Woodward discussed the idea of making MacDougal resident director of a "Department of Botany" at Tucson. MacDougal was willing, and Woodward presented the departmental proposal first at the executive committee meeting in October 1905 and then before the full Board in December.

MacDougal was an unassailable candidate, having recently become prominent as the ardent American champion of Hugo de Vries's theory of large and abrupt mutations. In his experiments at the New York Botanical Garden, MacDougal had won praise from the renowned European geneticist for supposed success (later seen to be mistaken) in creating a new species. MacDougal thus qualified as an "exceptional man" in the lexicon of the Institution.

Effective on January 1, 1906, MacDougal became director of Carnegie Institution's new Department of Botanical Research, situated at the Desert Laboratory. On the same day, Coville's role officially ended as the executive committee's confidential advisor in botany. MacDougal, who was clearly Woodward's man (not the executive committee's), would lead the Carnegie plant biologists for more than two decades.

MacDougal promptly went to Tucson, where in the next year or two facilities were improved, new lands were fenced in, and the main building received a new wing. Cannon stayed on, two additional staff scientists were added, and the resourceful Godfrey Sykes, a transplanted Britisher, began an adventurous two decades at the Department as engineer and field explorer. (Earlier, Sykes and MacDougal had explored the Colorado River delta.) Programs to collect climate and soil data at sites over the Tucson region were expanded, and in the next few years, field stations, or "plantations," were established at varying elevations in the Santa Catalina mountains to the north. Some of the mountain sites were accessible only by pack train.

Daniel T. MacDougal, c. 1903

The Luther Burbank Episode

Part of the case for MacDougal's appointment had been to help in managing the Institution's support of Luther Burbank (1849–1926), the renowned plant breeder. Although not scientifically trained, Burbank had gained fame for success in developing improved varieties of plums, grapes, berries, and potatoes. Burbank needed financial support to operate his plantations at Santa Rosa, California, and the Carnegie trustees liked the idea of studying the methods of this "exceptional man" and bringing them into the scientific literature. The best way to do this, MacDougal and Woodward agreed, was to send young investigators to Burbank to learn the master's methods. But Burbank, who worked long hours and was jealous of his time, proved an uncommunicative teacher. Thus several short-term proteges, including William Cannon, achieved little.

In May 1906, MacDougal and Charles B. Davenport, director of Carnegie's Department of Experimental Evolution, New York, visited Burbank and arranged for Burbank's extended cooperation with George Shull, later renowned for his experiments with hybrid corn at Davenport's Department.

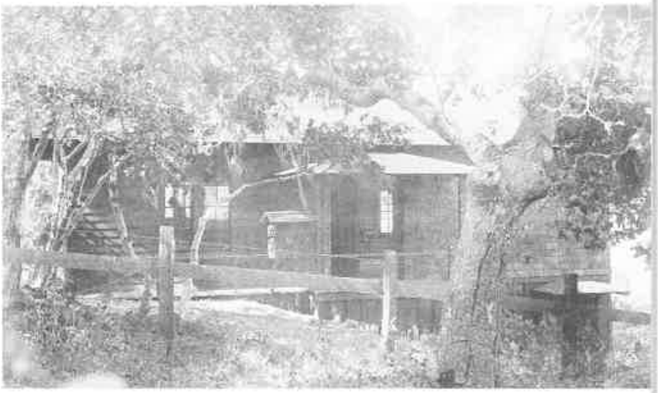
Shull soon determined that Burbank's methods were essentially those of the traditional breeder, who obtained desired traits by cross-breeding selected specimens over several generations. Burbank's success reflected the massive extent of his trial crossings, his use of many unusual varieties obtained worldwide, and his own trained instincts. To Shull, Burbank's crossing techniques and records were not meticulous, so that results—as tests of Mendel's laws, for example—were scientifically meaningless. In short, Burbank was an artist, not a scientist.

Shull gave up after several visits, and the Institution's leaders became disillusioned over Burbank's profit-seeking outside dealings. Woodward, however, in opposition to the executive committee, convinced the full Board in late 1908 to continue the Burbank grant. Andrew Carnegie, who attended the Board's meeting, spoke warmly on behalf of Burbank's work and its potential economic benefit. Even so, the ballot supporting Woodward's recommendation was well short of unanimous, and two years later Woodward acquiesced as the Institution ended its arrangement with Burbank.

At the Desert Laboratory, 1906. Seated (from left): Charles B. Davenport, Robert S. Woodward, D. T. MacDougal, George H. Shull. Standing: Godfrey Sykes, William A. Cannon, Burton E. Livingston, and F. E. Lloyd. Davenport and Shull were visiting from the Institution's Department of Experimental Evolution at Cold Spring Harbor, New York. Their itinerary included Luther Burbank's plantations in California.

Shull preserved his notes, professing the intention to complete a manuscript some day, but amid his own busy research career that day never came. The episode was a sour one for the Institution. The sums invested were significant—$10,000 annually, when the appropriation for the Desert Laboratory itself in 1909, for example (including salaries), was only $29,000. The experience strengthened the case for a tight departmental structure within the Institution and for caution in awarding grants to outside investigators working in their own environments.

Evolution of the Department



The Coastal Laboratory, Carmel.

For the year-round residents and summertime visitors, the Desert Laboratory was like a small village. Many lived in tent-houses on the Laboratory grounds, others commuted from town, and as years passed some staff members bought nearby desert lots and put up homes. Working facilities were gradually expanded and improved under MacDougal's direction, but they seldom went beyond the spartan. In use by 1911 were the original stone main lab, various single-story workshop, laboratory, and office buildings, several greenhouses, and an independent water supply designed by Godfrey Sykes. A 30-horsepower automobile, purchased in 1910, was specially fitted for carrying equipment on field trips.

The Department's Coastal Laboratory at Carmel, California, grew from summer studies there beginning in 1907 by William Cannon. (Cannon was working with plants obtained from Luther Burbank's plantations.) Cannon used a small building provided by the Carmel Development Company, and in 1908 the Company formally offered the Department four lots of land and a building. MacDougal envisioned that such a facility would be valuable for acclimatization experiments to supplement the desert and mountain-desert stations in Arizona. He noted: "Here we have an equable climate, high relative humidity, and low temperatures, while in the mountain locations, all these features go to extremes."

The Carnegie trustees formally accepted the gift in December 1908. The Carmel grounds included a well-watered garden, wooded slopes, and a hilltop area. The new building, paid for by the Development Company, had two main rooms. A small additional tract was purchased in 1911. The "Acclimatization Laboratory," renamed the Coastal Laboratory in 1913, became a favored location for research, and MacDougal and others often spent the summer months there away from the scorching heat of Tucson. MacDougal wrote that the site was "an admirable one both for experimentation and literary effort."

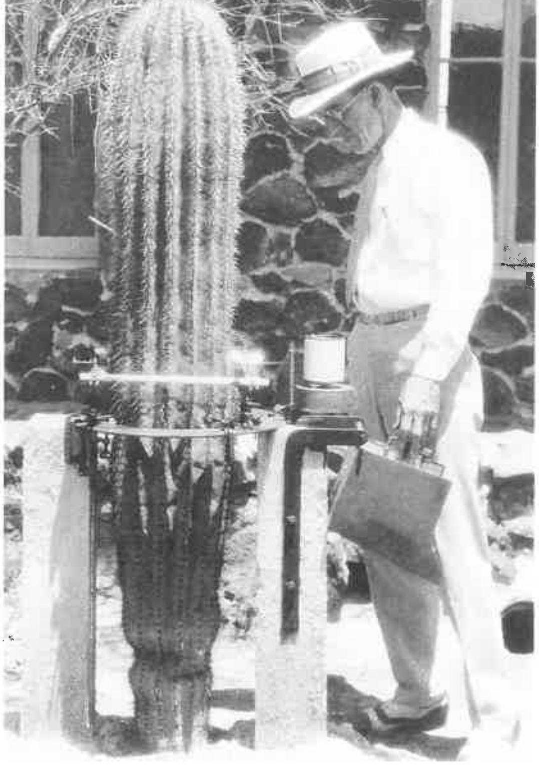
There was no visiting or advisory committee to the Department. Woodward came every year or so, trustees almost never except for trustee Cleveland Dodge, who reported enthusiastically after visits to Tucson in 1908 and 1911. Andrew Carnegie never visited but spoke proudly of the work being done at the Desert Laboratory.

All was not well, however, in relations between MacDougal and Woodward. Although Woodward had made MacDougal his first major appointee and had warmly praised him in the 1907 and 1908 trustee meetings, examples of acrimony began to mar their correspondence. Woodward saw the plant scientists as insensitive to the Institution's financial limits, and he belabored MacDougal with the importance of showing the trustees that administration was tight, indeed austere.

Woodward deleted increases in MacDougal's own salary from the latter's early budget proposals. In 1910, complaining about the manner of several purchases, Woodward warned MacDougal, "...let it be distinctly understood that there be no recurrence of such questionable acts. I shall certainly not hesitate to take such extreme action as may be necessary in cases of this kind." MacDougal did not always back down when thus challenged, and chilly exchanges sometimes ensued. Woodward later compared MacDougal to a "Tammany politician seeking, to use the politician's phrase, to work the Institution for all it is worth."

Shreve and Clements: the Giants in Plant Ecology

MacDougal was unmistakably successful in his appointments. In late 1906, he proposed that Forrest Shreve (1878–1950), a professor of botany at Woman's College (Goucher) in Baltimore, be added to the Department. Shreve came to the Desert Laboratory in 1908, and his seldom-interrupted work there until his official retirement in 1945 would, more than any other, symbolize the mainstream of the Laboratory's work. Frederic E. Clements (1874–1945) came to the Desert Laboratory in 1913 as a summertime visitor; a few years later, upon MacDougal's recommendation, Clements became a full-time research associate of the Institution, glad to be freed from the chores of university teaching. For many years thereafter, Clements would lead a Carnegie-funded program at the Institution's Alpine Laboratory, Colorado, and at gardens obtained by Clements in Santa Barbara, California.



Forrest Shreve reading the dendrograph record of a cactus. The instrument gave a continuous record of plant circumference showing seasonal and daily fluctuations due to water balance inside the plant.

Shreve and Clements were both outdoorsmen, whose choice of life's work reflected sincere devotion to nature and to understanding it. Shreve was a Marylander, whose deep interest in the ecology of plants led him to the Ph.D. at Johns Hopkins (1905). Prior to his move West, he shared in the preparation of a monumental volume on the plant life of Maryland, and he made several extended trips to Jamaica, investigating tropical plant life. Clements, a born westerner raised in Nebraska, obtained his Ph.D. at the state university with a thesis on Nebraska's evolutionary plant geography. As a faculty member at the Universities of Nebraska and Minnesota, he spent his summers traveling across the West and working at his plot in Pikes Peak (which was later expanded and became the Alpine Laboratory). Even before his Carnegie appointment, Clements had won a reputation for his original research and writing on the ecology of the West, including some of science's earliest field transplant experiments.

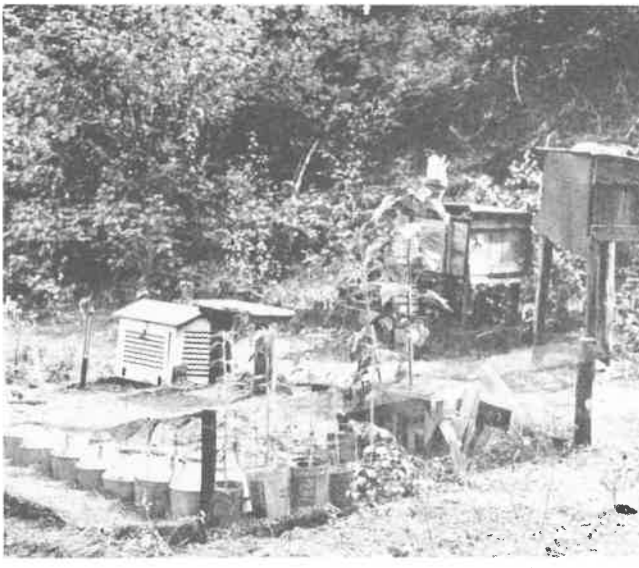
The two men could scarcely have been more different in temperament. If Shreve seemed entirely uninterested in self-promotion or the realm of science politics, Clements courted and capitalized on his fame. If Clements was a tireless organizer of fresh endeavors, Shreve was undriven, generally content to pursue his own goals at his own pace. Both had wives named Edith, and both Ediths were themselves plant scientists. Edith Clements was primarily helpmate to her husband in his research, while Edith Shreve always worked on independent topics. (Forrest Shreve did the couple's cooking.)

Clements was never hesitant with his ideas, believing that his own concepts were "of universal application"—i.e., they were "the only complete and adequate view of vegetation." His texts were often heavy with jargon devised by himself. Shreve carefully avoided using Clements's nomenclature and attacked Clements's ideas only indirectly and only within the scientific literature. Shreve, who was less famous in his lifetime but whose ideas have gained force with time, was satisfied to stay in a relatively private realm of disciplined and reflective work, allowing Clements the limelight. Clements took little public notice of Shreve. Both men were admired by those who knew them well.

The two differed fundamentally in their ways of interpreting nature. To Forrest Shreve, an understanding of plant ecology rested in the *individual* plant or species, and its ability to cope with the physical forces of nature. Habitat, to Shreve, was determined primarily by a plant's inherent capacity to function in the locale's climate and soil, less by a biological struggle with other individuals and species to prevail in a given niche. Neither cooperation nor conflict had much place in Shreve's ecological outlook.

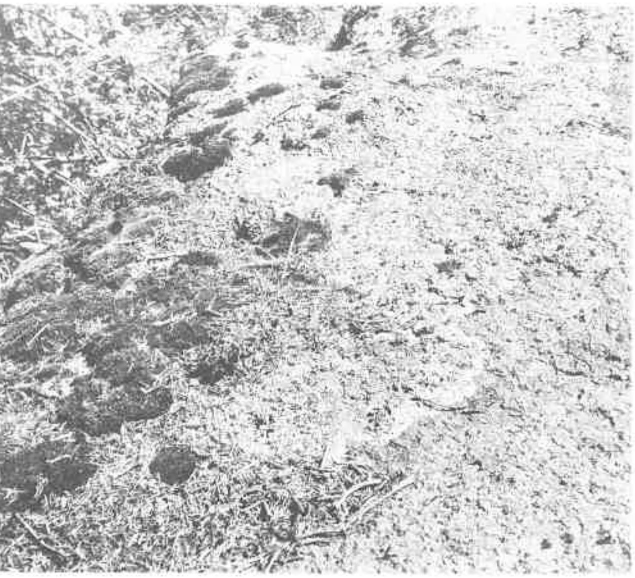
The Desert Laboratory grounds, the mountain plantations, and the Arizona terrain between, provided a superb arena for Shreve's work, offering distinctive regions of soil, climate, and vegetation. A few hundred feet in elevation, plant ecologists realized, meant measurable differences in climate. In his classic 1915 *Vegetation of a Desert Mountain Range*, Shreve correlated the gradients in environment and vegetation observed by his expert eye in the Arizona plantations; he showed that the factors most accurately explaining gradients in vegetation were those of temperature and moisture. Other factors—light exposure, soil, rainfall—correlated less directly with survivability.

Forrest and Edith Shreve later spent many summers at Carmel, where Forrest worked in



A full-sunshine plot for early experiments at the Alpine Laboratory. The containers at front left held growing sunflower plants, sealed at the base of the stem. Daily measurements of water loss and growth, compared with similar data obtained in half-shade and full-shade plots, gave indication of the effect of light intensity.

The Alpine Laboratory, located on the eastern slope of Pikes Peak. Experimental gardens were scattered at various elevations within the grounds and beyond. The Douglas fir and yellow pine of the locale represented a climax vegetation in Clementsian succession marking the climate of middle altitudes.



An example used by Frederic Clements of early stages of succession on a granite boulder, Pikes Peak. Crust-like lichens are at the right, followed by leafy ones, and then mosses where thin soil appears in crevices. As soil increases, various rock-breaking herbs appear, followed by grasses and ultimately shrubs and trees.

the coastal mountains, again correlating local vegetation with measurements of soil moisture, evaporation, and temperature, and comparing relations with those in the desert mountains of Arizona and the tropical mountains of Jamaica. Likewise in winters at Tucson, he continued to develop his "individualistic" concept of plant ecology.

To Frederic Clements, the vegetation in a given habitat was an instantaneous expression of a life cycle, or "succession," of a changing plant community. Starting with a denuded locale, stages of vegetation followed, each involving the invasion and establishment of newcomers, then competition and reaction, and finally stabilization. A particular set of climate and soil conditions (modified by a great variety of local influences), to Clements, entailed a predictable succession of stages, culminating in the natural climax formation. If for some reason conditions were returned to the original—by a landslide, for example—the identical progression would repeat, from invasive newcomers to stable climax vegetation. Clements likened the stages in succession to the developmental stages seen in an individual organism.

The scheme offered a structure for interpreting the relations between habitat and plant community, and Clements supported it with vast observational data. Competition played a critical role, and Clements once organized a systematic inquiry into plant competition, pitting one species against another in plots in Colorado and Nebraska. The conclusion, published in 1929, was that "competition plays the basic role in the community that food-making does in the plant."

Although Clements was easily the best-known plant ecologist of his time, later scientific assessments of Clementsian succession were generally harsh. The approach was too dogmatic for the modern taste, and in specific cases the arguments could be demolished in detail. The broad idea of succession and climax remains today in the biological textbooks, but it is hardly the ultimate design depicted by Clements. What largely remains for Clements's place in history is his role in awakening science to the intimate relation between plant and habitat, along with his sensible and influential views on land management and conservation, widely heard during the dust-bowl years in the Great Plains.

Forrest Shreve from the beginning resisted the sway of Clements. Shreve's independent concepts came to be shared by the ecologist Henry A. Gleason (New York Botanical Garden), whose 1926 and 1927 writings received wider attention than Shreve's earlier work. Gleason thus receives most of the credit for debunking Clements. But it remains striking that the contrary scholarship of Shreve and Clements coexisted within the single Carnegie Institution, to create much of the framework for modern plant ecology. To historian Robert P. McIntosh, the unusual case "is a tribute to the institution and its advisers."

The Department's Wider Scientific Program

The de Vries theory that evolution worked by large and sudden mutations offered an alternative to the gradual workings of Darwinian natural selection, which failed to explain large gaps in the fossil record. MacDougal at Tucson continued his earlier investigations into the matter, injecting chemicals into plant ovaries to induce mutations. (The chemicals were seen to replace the agent in nature responsible for mutations, the environment.) Other Desert Laboratory investigators also explored the mutations theory, including F. E. Lloyd (negative results) and W. L. Tower (who induced certain mutations in studies of beetles). Research elsewhere gradually overturned most of de Vries's ideas, however, and MacDougal's early prominence as their foremost champion passed.

MacDougal's energies went in other directions, and he had a hand in starting many of the Departments's later foci—experiments studying the behavior of cactus plants under controlled water deprivation, for example, extended investigations with Sykes and others into the ecology of the Salton Sea, and studies of the influence of light on plant function. In the studies of light, glass screens were specially developed to admit light of specified wavelengths only. MacDougal encouraged work on the desert rubber-plant guayule, of interest for commercial exploitation, including physiological studies and later genetic crossing experiments. Then in about 1918, MacDougal became interested in tree growth and its relation to climate, matters which he later pursued for many decades.

William A. Cannon devoted most of his attention to studies of the roots of desert plants, employing nondestructive methods to measure root growth in perennials. He became interested in the relations of root growth to gases in the soil, and did long-term experiments at Carmel into soil aeration and its physiological effects on plants. In extended explorations of arid regions of the Sahara, Australia, and southern Africa, he studied broad matters including root phenomena. Cannon became a victim (as he himself saw it) of the deteriorating relations between MacDougal and Woodward, and after Woodward's retirement MacDougal forced Cannon's resignation. Cannon in 1925 joined the Stanford University faculty, where he sometimes collaborated with Carnegie scientists and received occasional Carnegie grant support.

Various studies at the Desert, Coastal, and Alpine Laboratories entailed transplant experiments. In such work, plants native to a given

The Desert Botanical Laboratory, c. 1920. Looking to the north. (Credit: Arizona Historical Society, Tucson.)

environment could be studied in different habitats, or plants native to different environments could be studied in a common habitat. The possible experiments were unlimited for getting at the interaction of environment with plant form and function, the nature of species, and the possible inheritance of acquired characteristics. Satellite gardens, typically at varying elevation, were maintained both inside and outside the grounds of the three main Laboratories.

One of MacDougal's most distinguished recruits was Herman A. Spoehr (1885–1954). During a two-hour meeting in Chicago in 1909, the two men talked over the approach being taken at the Desert Laboratory and the possibilities for combining the largely outdoors research there with "a finely equipped technical laboratory." Afterwards, MacDougal wrote to Woodward, "I am disposed to believe that he is our man." Spoehr accepted the appointment as staff member the next year and brought to Tucson his experiments on the action of light in producing chemical changes in extracts of plant material. The idea was to test the various theories on photosynthesis, and Spoehr concluded that these theories were deficient.

During 1916–1918, Spoehr organized a systematic study of the carbohydrate economy of cacti "to gather data and some necessary facts which could be brought to converge for an attack on the problems of photosynthesis." Samples of tissue from living cacti were brought indoors and analyzed chemically; measurements of the various carbohydrates revealed large changes with season, water-content, and temperature. Later, Spoehr and J. M. McGee carried out experiments measuring respiration and photosynthesis rates against such variables as

H. A. Spoehr

time, illumination, and nutrient use.

By 1923, Spoehr knew that photosynthesis probably entailed many coupled reactions. Rejecting the various theoretical "speculations" on the subject, Spoehr wrote that "the only method which promises any real advance is the experimental one." Spoehr was unchallenged as the leading investigator in photosynthesis in this country, and his 1926 volume, *Photosynthesis*, remained for well over a decade the world's foremost treatment of the topic.

In his leadership of the Department of Botanical Research, MacDougal scored well in the ways that matter. He formed an able and enthusiastic staff, and he provided that staff the environment, tools, and encouragement to do the best work of which they were capable. Although the achievements of Shreve, Spoehr, and Clements surpassed his own, MacDougal gave no indication of jealousy. MacDougal liked to regard those around him as fellow workers, not assistants, and he held the reputation as the first to arrive mornings at the office or laboratory. He was an energetic if not meticulous administrator, though he was not always politic in his relations with the Institution's president. Although both promoter and builder, MacDougal was unquestionably more the latter.

The Reorganization in 1928

As the Institution's new president in 1921, John C. Merriam (1869–1945) was not one to ignore problems. Early, he turned his attention to the seeming organizational disorder among the plant biologists, i.e., primarily the separation of the Clements-led program in Colorado and Santa Barbara from MacDougal's Department of Botanical Research at Tucson and Carmel. Merriam suspected that the situation made it difficult to attain the highest quality and most significant science per dollar. As always, the Institution had no funds to waste; it now operated ten departments, and its annual spending often exceeded revenues. (The plant biologists' share of the Institution's budget was slightly over six percent, of which Clements's program required about a third.)

In considering reform, Merriam faced strong, opposing pressures. Clements, on the one hand, had long urged further expansion of his program and its conversion to full departmental status. His proposals came replete with the names of university scientists who would be added as full-time Carnegie staff members. The canyon and nearby mountain locales at Santa Barbara, he wrote, in combination with the Colorado sites, offered "matchless opportunity for the study of life in its natural environment." Clements's prestige was hard to withstand.

Meanwhile, Herman Spoehr's laboratory-oriented approach to the physiology of photosynthesis was beginning to overshadow the other work of the Department. Spoehr moved his laboratory from Tucson to a new building in Carmel, completed in 1921, featuring underground constant-temperature rooms. In 1923 the Department was renamed the Laboratory of Plant Physiology, clearly suggesting the primacy of Spoehr's program over the outdoors-oriented work of Shreve and others still at the Desert Laboratory. Spoehr, however, was not satisfied by his working situation, and in 1923, Merriam and MacDougal agreed that Spoehr's work was "important to the Institution," and that in order to retain him Spoehr's salary should be raised.

John C. Merriam

The Division of Plant Biology's main laboratory building, photographed upon its completion at Stanford in September 1929.

Meeting with Merriam in April 1925, Spoehr complained about facilities and isolation at Carmel and again spoke of leaving. Merriam responded by offering money for building expansion, journal subscriptions, and additional research assistants, along with "an adminstrative relation that would make it possible for Dr. Spoehr to have the freedom necessary for development of his researches." Spoehr agreed to stay.

Fortified by the report of a committee set up in 1926 chaired by Spoehr, Merriam in fall 1927 was ready to move for unification:

> The fact that good work is being done and would be done without change does not dim our vision regarding further possibilities nor does it relieve us of responsibility for making such changes....

In his internal memo, Merriam depicted "two groups of interests"—i.e., the "physiological" and the "ecological" programs, apparently represented by Spoehr on the one hand and Clements or Shreve on the other. Which group should prevail in the unification? Merriam concluded that

> ...there are many reasons why leadership might rest with a representative of the group of investigators in the more fundamental field, that is, in physiology as expressed through the study of the physical and chemical aspects of physiology.

The new Division of Plant Biology came into existence on January 1, 1928. Following the recommendations of the Spoehr committee, the main location was to be on five acres of leased land (later enlarged) on the campus of Stanford University, and planning for a central laboratory and experimental gardens began at once. The chairman of the new Division, through whom all business including annual budget requests must pass, was H. A. Spoehr.

Spoehr's own lab was shifted to the new building at Stanford, which was completed in July 1929, six months after ground-breaking. A younger investigator, Harvey Monroe Hall, who had once worked with Clements, was to head a section at Stanford on "experimental taxonomy," thereby extending a field and transplant program already started by Hall in California. MacDougal would stay at Carmel continuing his tree-growth studies, Shreve would administer scaled-down activities at the Desert Laboratory, and Clements would continue his programs in Colorado and Santa Barbara, all as sections under the Spoehr-led Division.

The Outlook in 1928

The Carnegie Institution's 25-year investment in plant biology had produced worthy dividends, including contributions by dozens of investigators in the opening of the field of plant ecology. Frederic Clements stood the acknowledged head of the discipline, but the challenge to the Clementsian paradigm was already apparent, having been challenged early, albeit softly, by Shreve.

By 1928, Mendel's laws and many ramifications had become accepted by scientists. The Carnegie plant biologists had contributed only peripherally in this development, but now stood poised to make definitive contributions in the studies planned by Harvey Hall.

Historians of science have detected a trend among young biologists of the early 20th century away from the larger and more-speculative questions in evolution and heredity. The new breed tended to reduce matters to smaller questions, often physiological in nature, which could be solved in laboratory studies. How, in detail, did the components of organisms function? Increasingly, biologists were urged to find ways to employ the quantitative and experimental. Carnegie Institution's decision to build the new laboratory facility at Stanford and give preeminence to the work of Spoehr there, was a major step in the development of these trends.

Part II. To 1973

The completion of the new central laboratory in 1929 began an extended era of stability in leadership and program for the Carnegie plant biologists. Herman A. Spoehr proved an able and universally respected leader, though a somewhat autocratic one by later standards, whose firm hand gave continuity and clear vision in research programs. Spoehr's successor in 1947, C. Stacy French, brought a looser style of leadership and wider links to the worldwide research community. The ability and integrity of both directors earned the confidence of the Institution's presidents—Merriam to 1938, Vannevar Bush to 1955, and Caryl Haskins to 1971. In contrast to Merriam's closer involvement, Bush and Haskins practiced a knowledgeable, helpful, but largely hands-off oversight of the affairs of the Department.

For the first decade or so, scaled-down activities continued at the Desert, Alpine, and Coastal Laboratories, affording facilities for the continuing work of Shreve, Clements, and MacDougal. All three Laboratories were closed under Bush, along with the Division's support of outside research associates. The changes registered the conviction, shared by Spoehr and Bush, that the best and most promising science was that being done at Stanford. To reflect the streamlining, the Division in 1951 was renamed the Department of Plant Biology.

Two principal directions of research remained. The work in experimental taxonomy (later called physiological ecology), begun by Harvey Hall, continued the long-standing Carnegie interest in plant ecology and in questions of environment, adaptation, and heredity. Meanwhile, the program of the photosynthesis group (later called the biochemistry group) reflected the personal research interests of, and was led directly by, first Spoehr and then French.

Trees, Climate, Paleobotany

MacDougal's Tree Studies. After his retirement as director in 1928, Daniel T. MacDougal continued his tree studies at Carmel. Using his dendrograph instrument to measure the circumference of tree trunks, MacDougal could compare diurnal changes with water supply, temperature, and other environmental variables, and study longer-term seasonal and annual growth patterns. He was also interested in internal movements of fluids, including gases in solution in the sap-stream. By means of boreholes, internal pressures were measured, dyes injected, and sap withdrawn; suction was measured at cut ends of roots, branches, and tree-tops.

Suspicious that MacDougal's work had become mainly an exercise in accumulating data, Merriam in 1930 made it clear to F. W. Haasis, a newly appointed research associate at Carmel, that future emphasis should be on the interpretation of existing data. MacDougal and Haasis indeed prepared a series of summarizing publications in the next several years.

Vannevar Bush

But MacDougal was not ready to stop. One reviewer, writing in 1939, wrote that "one cannot but marvel in the energy with which the veteran, now in his 74th year, continues his researches." The Coastal Laboratory facilities were closed in 1940, but the indomitable one continued his regular measurements and in 1952 wrote to Vannevar Bush offering a fresh manuscript for publication. The Institution declined the opportunity in the belief that MacDougal's dendrograph measurements were imprecise by modern standards.

Tree Rings and Climate. Early in the century, Andrew E. Douglass, an astronomer of the University of Arizona, became interested in the message of tree rings. Douglass became superbly successful in using tree-ring information to date ancient wood. By cross-correlating annual rings in many specimens, including a wide collection of fossils, a continuous record of recognizable ring patterns reaching back nearly 2,000 years was developed; with the ring record as a reference, many wooden samples from the ancient Indians of the American Southwest were conclusively dated.

But Douglass was less successful in finding cycles of climate in the tree-ring data. Carnegie's MacDougal, Clements, and Merriam joined Douglass in the hope that climate could be correlated with the sunspot cycle, and perhaps help in long-range weather prediction and in society's use of farm and range lands. During the 1920s and 30s, Carnegie support allowed extension of Douglass's work to the Pacific redwoods, the hiring of a full-time scientific assistant, and the provision of auxiliary work space at the Desert Laboratory. Carnegie also convened several conferences on cyclicity, attended by Carnegie plant biologists and astronomers as well as outside scientists in other disciplines.

Then in 1935 Douglass became a full-time Carnegie research associate, an arrangement allowing him to step down as director of Arizona's Steward Observatory and launch a three-year assault on the climatological question. The work hinged heavily on the analytical determination of cyclicity in the tree-ring data, and Douglass developed an optical-mechanical "cyclograph" to replace the vastly time-consuming mathematical analysis.

About to begin his Carnegie presidency and uncertain in judging Douglass's claims of cyclicity, Vannevar Bush in 1938 asked the distinguished mathematician Norbert Wiener of M.I.T. to study Douglass's analyses. Wiener reported that although the cyclograph was "certainly an ingenious instrument for preliminary examination of data for hidden periodicities," in his opinion the overall working of the data had been very sloppy. Wiener gravely doubted the cyclicities seen by Douglass.

Carnegie support of Douglass's work ended soon afterwards. Douglass ended his career at the University of Arizona's Laboratory of Tree Ring Research, an entity created to harbor his large collection of tree sections.

Paleobotany. As president, Merriam initiated Carnegie Institution support of various investigators in paleontology, Merriam's own field. Thus the paleobotanist Ralph W. Chaney became a full-time research associate of the Institution in 1922, his work administered by the Division of Plant Biology. From his base at Berkeley, Chaney often interacted with the Carnegie plant biologists.

Chaney studied ancient plant distribution, much as modern plant ecologists studied modern distribution. Wishing to understand ancient climates and ancient plant migrations, he worked widely over the globe, most intensively in the northwestern United States. Chaney joined Douglass in studying ring growth of petrified trees in the Yellowstone, and he collaborated briefly with Clements in writing about the virtually new field of "paleoecology." The latter partnership was troubled, as Chaney found himself unable to agree with Clements's more-speculative interpretations.

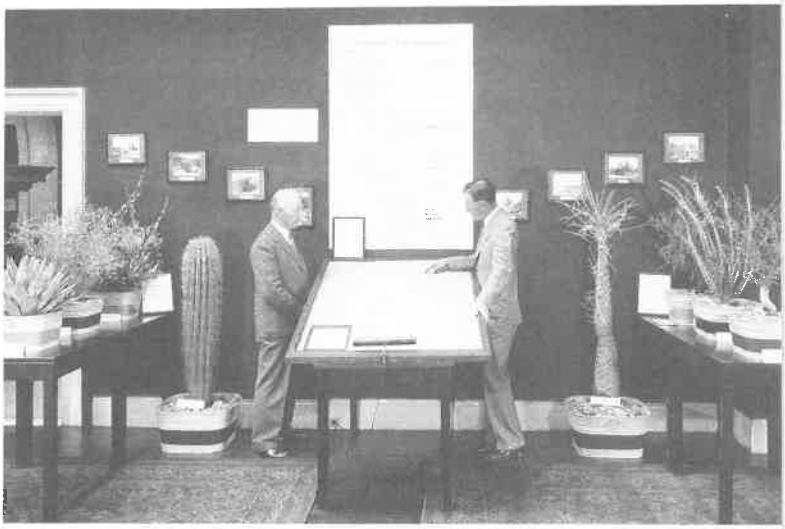
Chaney left full-time Carnegie service in 1931 to become chairman of the Department of Paleontology at Berkeley. The Institution continued to pay his research expenses until 1956.

Like Merriam, Chaney was a leader in the Save-the-Redwoods League. When in 1948 he learned that a small population of Metasequoia trees, supposedly long extinct, had been found living in China, Chaney made a laborious trip into remote Szechuan, where he indeed found these close ancestors of the California redwoods. Chaney brought back seeds, propagated seedlings from them, and planted Metasequoias at hospitable sites in America, including the Carnegie campus at Stanford.

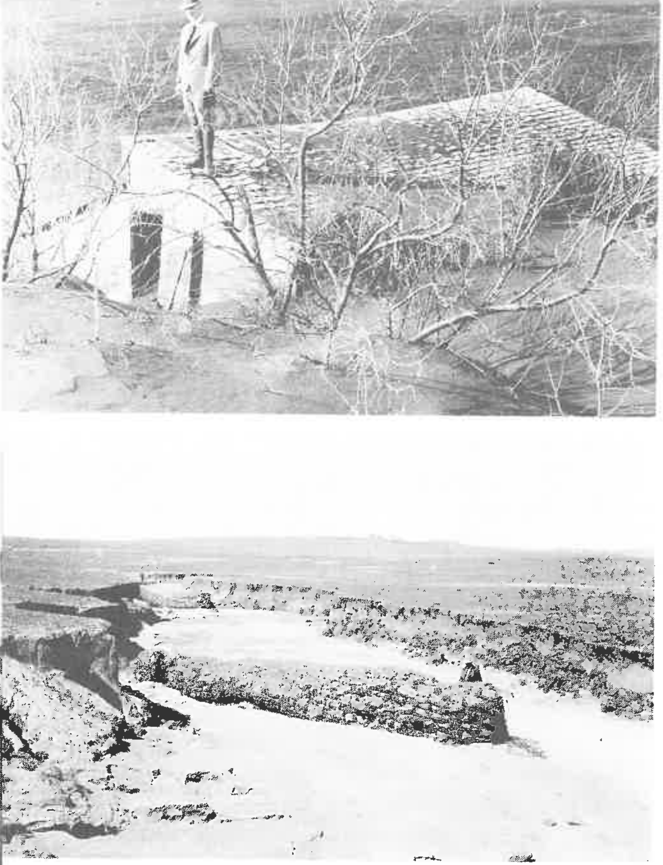
Shreve and Clements: Late Years at the Desert and Alpine Laboratories

After 1928, the scaled-down Desert Laboratory became primarily a base for the work of Forrest Shreve, his few associates, and declining numbers of summertime visitors. Merriam and Spoehr recognized the quality of Shreve's past work, and both acknowledged that there were "great and important" research questions in the desert. But both doubted, as Merriam put it, whether Shreve had "the unswerving purpose required for bringing a really great program to success."

T. D. Mallery, an associate at the Desert Laboratory, reads rainfall collector (at right) by pouring contents into a graduated flask and allowing the oil, used to prevent evaporation, to rise.



Forrest Shreve (right), attending the 1935 Desert Laboratory exhibit at the Carnegie Institution of Washington building in Washington.



Frederic Clements, top, amid dunes of soil in the Great Plains, mid-1930s. Below, overgrazed watershed in eastern Colorado. Clements was widely heard in urging improved land-use policies.

Prodded by Merriam and Spoehr toward a more focused effort, Shreve intensified a field program compiling the vegetation of the Sonoran Desert. (The book, published by the Institution in 1951, became a contribution of lasting value.) Shreve's requests to increase the staff ran in the face of the Institution's fiscal stress during the Great Depression, and his recommendation to start a major interdisciplinary effort in desert studies was further doomed by Merriam's belief that Shreve would be a poor administrator. Merriam and Spoehr between themselves in the early 1930s discussed the possibility of closing the Desert Laboratory.

Shreve in 1934 successfully argued against closing the Laboratory, writing that his own research would be seriously set back and citing the importance of continuing to protect the natural state of the Laboratory's extensive fenced-in grounds. But Shreve was unpersuasive in what may have been a final opportunity to change the course of events—a 1939 visit to the Desert Laboratory by Lewis Weed, chairman of the trustees' committee on the biological sciences and an individual often consulted by Bush. Weed, according to Spoehr, came away annoyed by Shreve's long and negative complainings of inadequate facilities.

A few months later, Vannevar Bush informed Spoehr that "curtailment" of the Desert Laboratory was to be immediately effected, "under the pressure of lowered income." The buildings and land were turned over in 1940 to the U. S. Forest Service, which two decades later sold them to the University of Arizona for classroom and office use.

Frederic Clements meanwhile presented different kinds of problems. Anguished by his subordination to Spoehr in the 1928 reorganization, Clements soon afterwards told Merriam that Spoehr was making it difficult to carry out his work. Clements said he needed independence and a direct line to Merriam. Merriam tried to keep things patched up, but finally told Clements that any requests sent directly to the president would be promptly passed to Spoehr.

The Carnegie leaders were also troubled by some of Clements's science. Spoehr and the members of the experimental taxonomy group at Stanford challenged the rigor of the experimental work at the Alpine Laboratory and at Santa Barbara. They doubted, for example, Clements's claim to have converted species experimentally. Despite repeated challenge, Clements neither published data from the relevant experiments nor, as a suggested alternative, was willing to provide his evidence for review by the other Carnegie plant biologists. Spoehr and Bush also mistrusted Clements's 1940 interpretation linking the recent drought decade with sunspot numbers, though ultimately, for the sake of academic freedom, the material was kept in the Carnegie Year Book.

Clements retired from active service in October 1941. Shortly afterwards, the Institution suspended activities at the Alpine Laboratory and transferred the property to Clements for his post-retirement studies. Clements died in 1945.

The Experimental Taxonomy Group

As a plant taxonomist, Harvey Monroe Hall (1874–1932) was dedicated to the careful and exhaustive morphological analysis of specimens. His early collaboration with Frederic Clements at the Alpine Laboratory in 1918–1919 had been difficult, Hall deeming that the transplant experiments were not meticulous and disagreeing with Clements's inclination to view acquired characteristics as heritable, i.e., the lamarckian view. Hall returned to Berkeley, where he continued to receive full funding under Clements's budget, although most of his research was independent. Hall rose in the esteem of both Spoehr at Carmel and Merriam, who often spent time at Berkeley for periods of research. Hall served with Spoehr on the 1926 committee recommending the reorganization of the Carnegie plant biologists, moved to Stanford to head the experimental taxonomy section in 1929, and briefly served as the Division's acting chairman during Spoehr's short-lived resignation during 1930–1931 to join the Rockefeller Foundation.

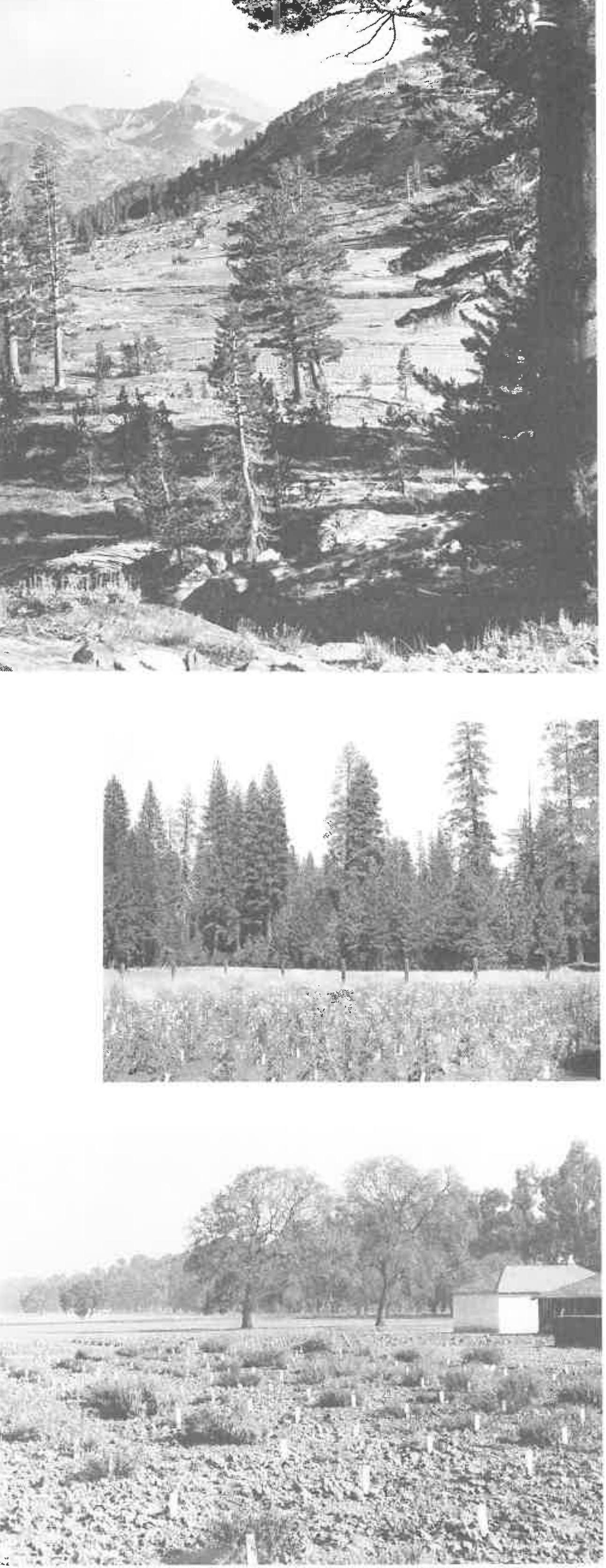
In organizing the new transplant program in California, Hall in 1926 Hall recruited two younger assistants—William Hiesey and David Keck. By 1929 three main stations were in use—the gardens at Stanford (elevation 30 meters), Mather station on the western slopes of the Sierra (elevation 1400 meters), and the Timberline station, beyond the divide (elevation 3050 meters). In 1931, Hall recruited the Danish geneticist Jens Clausen.

Hall's sudden death in 1932 left the program in the hands of Clausen, Keck, and Hiesey. The three-man team carried on Hall's general plan, their approach strongly endorsed by leading outside scientists at a three-day conference convened by Spoehr in July 1934. An informal division of responsibility evolved: the physiologist Hiesey was the most active at the field stations, Keck in the taxonomic analyses, and Clausen (the unofficial leader) in cytological and genetic work. A crucial advantage was the sustained funding assured by Spoehr's firm support.

Above: Jens Clausen and William Hiesey. Right: Harvey M. Hall.

The magnitude of the horticultural, gardening, and data-gathering effort, involving thousands of individual plants over more than two decades, was enormous. A transplant experiment characteristically used clones from a single individual. The selected parent was taken from its habitat, carefully washed, and divided vegetatively; each propagule was potted and established in a nursery. When strong enough, the clones were planted at the different stations. (Clones from plants dug in the summer were usually ready for the field the next spring.) Measurements were then taken at regular intervals, and all data meticulously recorded.

Hundreds of species were tried, leading to



From top to bottom: the experimental and transplant gardens at Timberline, Mather, and Stanford.

concentration on those most valuable scientifically and most suitable for transplanting. One of the most useful genera was *Potentilla*, a leafed plant typically about a half-meter tall found in many varieties over western North America and much of the rest of the world. Clones from individuals native to varied habitats were studied at the three locations, yielding vast morphological and growth data, including many photographs. The object was to isolate the effects of heredity and environment.

Results from the transplant studies were integrated with genetic and cytological information. The genetics work entailed crosses to test relatedness of types by their ability to produce hybrid offspring viable over several generations. Cytological evidence came from inspecting and counting the chromosomes by microscope. (Chromosome number was both itself a morphological characteristic and also a direct indicator of genetic change.)

In the mid-1930s, Spoehr put heavy pressure on the group to focus and accelerate the work toward early publication. The result, reaching print in 1940, was the classic first of six volumes *Experimental Studies on the Nature of Species*. Therein, Clausen, Keck, and Hiesey presented conclusive evidence from *Potentilla* and other species, evidence which by virtue of the study's rigorous methodology at once ended many of the long-standing controversies involving environment, adaptation, and heredity.

Their conclusions by and large supported views of the "neo-Darwinians," thereby refuting most of the lamarckian viewpoint. Evolution, the Carnegie scientists wrote, has left plants in various stages of differentiation caused by diversity of environment. In a continuum of differentiation, the basic classification levels are those of ecotype, ecospecies, and cenospecies (roughly corresponding to variety, species, and genus). An individual plant grown away from its natural habitat might tolerate the new conditions and change characteristics within the range of its hereditary capacity for modification. Such changes, however, are reversed upon return to the original environment and are not passed to offspring. In short:

> We have no evidence that the direct influences of the environment produce fundamental hereditary changes in species, but major alterations in environments provide new habitats and refuges for the products of nature's continual experimentation among all the plant species that populate a given area.

A new species, the investigators concluded, can result from simple and gradual gene changes in geographical isolation, or from rapid changes. Indeed, an important part of the Clausen-Keck-Hiesey program was an attempt to demonstrate in experiments how a new species might be built.

A new species was indeed achieved, by means of amphiploidy, where the unequal numbers of chromosomes in two parents are combined in an offspring. The experimental organisms were two species of *Madia*, one having nine, the other eight, pairs of chromosomes. The two species were native to unlike habitats and had been isolated from one another in nature by the width of the Sacramento Valley.

The experimenters by hand-pollination achieved several first-generation hybrids having 17 chromosomes, nine from one parent, eight from the other. Although most of the first-generation hybrids were sterile, a few second-generation plants were achieved by self-pollinating, some having 17 chromosome pairs. The second-generation plants were then allowed to mutually pollinate, and multiple descendants were produced via natural meiosis through a fifth generation. The new species, *Madia nutrammi*, had 17 pairs of chromosomes, reproduced its own kind within the natural range of variation, and hybridized with no other species. It exceeded both original parent species in vigor while growing at the Stanford gardens.

The investigators also synthesized by amphiploidy a species of *Madia* which occurred in nature, along with an artificial species of *Layia*.

By demonstrating how amphiploidy could work in nature, Clausen, Keck, and Hiesey showed how two genomes could be rapidly combined to allow colonization of a new environment. Their claim of species building was scarcely the first, but it was among the earliest that have stood the test of time. The experiments are still sometimes cited popularly and in textbooks as evidence confirming the reality of evolution in nature.

During World War II, Clausen organized a wide program crossing range grasses (*Poa*) capable of self-reproduction (apomixis). The hope was to achieve genetically stable strains having improved yield and tolerance to extreme climate, thereby enhancing world food supply. Widespread collaboration was established with the U.S. Soil Conservation Service, various universities, and agricultural experiment stations. The work eventually stretched over two decades, and several self-reproducing (apomictic) derivatives of *Poa* were synthesized. None, however, were clearly superior in growth performance to parental lines.

The Leadership of Björkman. The group's outlook gradually turned to newer kinds of questions. What were the exact physiological responses within the plant that signified a broad adaptation to an environmental stress? How might these mechanisms of adaptation themselves have evolved? Such questions required different techniques—the use of controlled-growth chambers, the study of tissue cultures, and better quantitative measurements of photosynthesis.

The newer direction roughly coincided with the career of Olle Björkman (b. 1933), who came to Carnegie from Sweden in 1964, already known for his laboratory studies of adaptations in forest and alpine plants to various light intensities. In his first years at Carnegie, Björkman joined the physiological ecology group in major investigations of adaptation in *Mimulus*. The work built upon the group's recent analyses with *Potentilla*, showing that a given variation (in leaf length, for example) typically involved not a single gene but several linked genes. (The result suggested that crop improvement through genetic engineering in the future would be no simple matter.) Björkman also began collaborations with members of the Department's photosynthesis group in probing basic mechanisms of photosynthesis.

In 1966, in experiments studying the effect of ambient oxygen concentrations on photosynthesis, Björkman reported that CO_2 uptake (i.e., photosynthesis) is rapidly and markedly enhanced as oxygen pressure in the environment is reduced. (Conversely, increased oxygen pressures are inhibiting.) The effect was seen among diverse species of higher plants, without regard to light regime. The phenomenon was at once seen as important, as it appeared to bear on many aspects of photosynthesis; Björkman continued experiments to explain its mechanism.

Desert field work. (Olle Björkman at right.)

Following the retirements of Clausen and Hiesey, Björkman in 1969 became the unofficial leader of what was thereafter called the physiological ecology group. Joseph Berry joined the group the following year; Malcolm Nobs had earlier taken the place of Keck. Meanwhile, investigators elsewhere had discovered in certain plants a pathway for carbon fixation, called the C_4 pathway. (In contrast to the previously known C_3 pathway, the first product in CO_2 fixation in C_4 photosynthesis is a compound of four carbon atoms.) Björkman and Nobs immediately became interested in the implications of C_4 photosynthesis for the adaptation and natural selection of plants, and investigations of C_4-capable plants became a focal point of the group's work for several years.

The group chose two species of *Atriplex*, one found in coastal marshes and the other in semiarid regions. Only the latter possessed the C_4 capability. (Hall and Clements had long ago collaborated in an extensive analysis of the genus.) In 1969, Björkman and colleagues reported comparisons of CO_2 uptake in the two species at varying light exposure, temperature, and ambient levels of CO_2 and oxygen. They showed, for example, that the phenomenon of oxygen inhibition earlier discovered by Björkman appeared absent in the C_4 species. Nobs was successful in hybridizing the two species and then in growing second- and third-generation offspring, paving the way for further experimentation comparing the descendants with the original parents.

In physiological studies, the Carnegie workers showed that the C_4 does not replace the C_3 cycle but rather complements it, serving in effect as a CO_2-concentrating mechanism. Meanwhile in experiments in the extreme environment of Death Valley, the Carnegie investigators, with Stanford University colleagues, explored the remarkable photosynthetic capacity at very high temperatures of the C_4 species *Tidestromia oblongifolia*. Although the point was not often stated, always understood in such work was the hope that the capacity of C_4 plants for increased CO_2 fixation per water lost in transpiration might some day be applied in crop breeding.

By 1973, the old stations at Mather and Timberline were mostly used for research by university students. The physiological ecology group now depended heavily on the indoor controlled-growth facilities at the central laboratory; comparative work outdoors was done, often in collaboration with the Stanford University group, at experimental sites in Death Valley and at Bodega Head, California, which together provided extremes of hot desert and cool coastal regimes. The collaborators also converted a motor van into a mobile laboratory suitable for field use; gas-exchange measurements on the whole plant or the single leaf could be directly captured by an on-board computer.

The work of the Björkman-led group was in 1973 still at an early point. A growing commonality of interest with the photosynthesis group was detectable, seen in a recently initiated long-term joint study on adaptations of the photosynthetic apparatus to extremes of heat and dryness.

The Photosynthesis Group under Spoehr

In 1929, except for a recently formed group at Harvard under Robert Emerson, Spoehr and colleagues were the only group in the United States doing basic research in photosynthesis. Spoehr had led in studying the machinery of photosynthesis as a whole, measuring external inputs and outputs. But getting at the workings inside the plant was proving no easy matter. Spoehr wrote that understanding would not come from a single brilliant discovery but would instead be a stepwise process, to be fashioned from the work of many investigators.

Malcolm Nobs, with the C_3 *Atriplex triangularis* (seen at left) and the C_4 *Atriplex rosea*. The two species were used as parents in hybridization studies related to exploration of the C_4 photosynthetic capability.

Cooperative aspects thus strongly flavored the Carnegie assault on photosynthesis. At the Division's central laboratory in Stanford, Spoehr was surrounded by able colleagues James H. C. Smith, Harold H. Strain, and Harold W. Milner. All three men would remain on staff through the two decades of Spoehr's chairmanship. (The meticulous Milner often had the role of Spoehr's research assistant.) Group discussions were frequent, patterns of collaboration were fluid, a collegial spirit was preserved; Spoehr used his superior position mainly to insist that all work be done with excellence.

Once investigators at Stanford University, Berkeley, and Caltech took up photosynthesis, Spoehr initiated exchanges among all the West Coast groups, including visits and the sharing of data. Everyone knew what the others were working on. Spoehr also arranged Carnegie funding for several outside investigators whose interests were close to the Division's.

The whole range of photosynthetic activity was open for investigation. One approach was by the careful measurement of heat (i.e., energy exchange), which might reveal the timing and tell something of the nature of internal reactions during photosynthesis. Another was in studying the chemistry of plant carbohydrates, including interconversions of sugars and accompanying hydrogen ion concentrations. Increasingly important were experiments measuring effects of applied light, yielding "action spectra" showing the wavelengths associated with given reactions within the plant. Action spectra could be correlated with the absorption spectra of given pigments or enzymes, perhaps to reveal roles of pigments or enzymes in particular reactions. Experiments with extracts of plant material in solution, as opposed to experiments with living plants, raised hosts of technical and interpretive questions. Much of the work was with liquid cultures of algae, especially the green alga *Chlorella*, which became a widely used organism for studying photosynthesis.

Considerable effort in the early 1930s went into studying the yellow leaf pigments, mainly carotene and xanthophyll in their several forms, and their possible roles (perhaps paralleling that of chlorophyll in capturing the energy of sunlight). Smith, Spoehr, and Milner worked out the complex chemical structures of carotenes and studied the patterns of their absorption of light of various wavelength. For this work, the Division purified considerable quantities of carotene, chiefly from carrots and other plants grown in the Stanford gardens; quantities were also supplied to outside investigators, who were interested in the material's relation to the animal nutrient vitamin A. Harold Strain devised a chromatographic procedure to separate the different forms of carotene; various applications from Strain's continued development of chromatography later came into wide use at other laboratories.

Although Spoehr's relations with Merriam were harmonious, the photosynthesis group was not exempt from the president's proddings. Merriam in 1934 told Spoehr that the photosynthesis work, though it was one of the most important of the Institution's activities, seemed to be lagging. Merriam questioned whether or not results were commensurate with the effort, interest, and ability applied.

Perhaps reacting to this pressure, Spoehr in 1935 acknowledged that the work on carotenoids had taken longer than expected, but that it had finally reached a point that other directions could now be taken. In one of several new ventures, Robert Emerson, then at Caltech, in late 1937 came to Carnegie as a research associate to lead a planned three-year program with *Chlorella*. The idea was to pin down the energy relations of photosynthesis—i.e., the amount of light required per CO_2 molecule reduced, a value known only from rudimentary experiments years earlier. Emerson had talked often with the Carnegie group on such matters, and had

The Department's mobile laboratory.

worked previously at the Coastal Laboratory. Instrument-makers of Carnegie's Mount Wilson Observatory helped in building the light-generating and measuring devices needed for the effort.

Emerson's measurements at Carnegie showed that the light requirements in photosynthesis were greater than had been understood, and therefore that the series of steps in the photosynthetic process was longer than previously supposed. Of greater significance was another result—the observation of a severe drop, or "red drop," in photosynthetic efficiency at the far red wavelengths. Emerson soon afterwards determined that the photosynthetic rate in far red light could be enhanced by supplemental light from shorter wavelengths—the "Emerson enhancement effect." It thus appeared that two separate pigment systems were at work, absorbing preferentially at different wavelengths. It was an important step toward the general recognition of two distinct photoreactions in plant photosynthesis.

The Division also pioneeered in the early use of radioactive tracers to study processes inside the plant. With Vannevar Bush's encouragement, Spoehr, having been frustrated in his earlier efforts to disentangle the chemical reactions involved in CO_2 absorption, explored the possible use of radioactive carbon to label the original CO_2 carbon atoms and trace them during processing and use inside the plant. Although biologists at Berkeley had already started a similar effort, Spoehr arranged a collaborative venture with Carnegie's DTM, where several early nuclear generators had been assembled. James Smith in 1939 spent several months working at DTM, reaching a rudimentary ability to measure CO_2 molecules inside the leaf. Thus encouraged, Spoehr and Bush discussed building an inexpensive cyclotron facility at the Division as a source of radioactive material. The war years interrupted the venture, which was not resumed afterwards because other groups were by then far ahead.

Bodega Head, California.

A major wartime effort to isolate an antibacterial substance from *Chlorella* led to later experiments by Spoehr and Milner studying how the protein content of *Chlorella* could be varied by environmental factors. The idea emerged that *Chlorella*, grown not in soil but in cement tanks, might offer a useful foodstuff in land-poor countries. Bush agreed, and Carnegie Institution and Carnegie Corporation paid a contracting firm to build and operate a *Chlorella*-producing pilot plant in Massachusetts. Troubled by contamination in the growth tanks, the venture yielded disappointing results, published in 1953. One Carnegie scientist wryly noted that the effort "had been run by engineers not biologists."

French as Leader of the Department and Photosynthesis Group

Believing in 1946 that the Division's leadership should pass to new hands, Spoehr proposed stepping down early. To serve as the new leader, Spoehr recommended C. Stacy French (b. 1907), then at the University of Minnesota, whose research fit well with that of the Division. (French had explored the recently discovered reaction where under

C. Stacy French, left, and Harold Milner.

illumination oxygen is liberated from chloroplasts suspended in solution, resembling the evolution of oxygen in natural photosynthesis.) Spoehr had watched French's career ever since French first visited the Stanford lab in 1934, fresh from his Ph.D. work at Harvard.

French spent a month at the Division in summer 1946 and met with Bush and trustee Alfred Loomis later in the year. In accepting the Carnegie appointment, French obtained a free hand to seek closer relations with Stanford University, to include the use of graduate students at the Division. Thus in July 1947 French became the Division's "director" (Spoehr had been "chairman"), though the new title would scarcely fit French's unauthoritative leadership style. Spoehr, at age 62, returned to full-time investigation.

French's outgoing personality was reflected in a widening of the Division's external relations. Important long-term collaborations evolved with leading groups in the Netherlands, Germany, Scandinavia, and Japan. French was very pleased with the strong postdoctoral program, introduced in all the Institution's departments under Bush, and deemed that the postdocs and visiting investigators, who often brought new techniques and ideas from other labs, contributed more to the Department than they carried away. Every few years, French visited the leading labs of Europe to renew professional ties and recruit the best young people. Despite French's early intentions, however, only Björkman's group developed strong links to Stanford University, and predoctoral students were not yet regularly seen at the Carnegie Department.

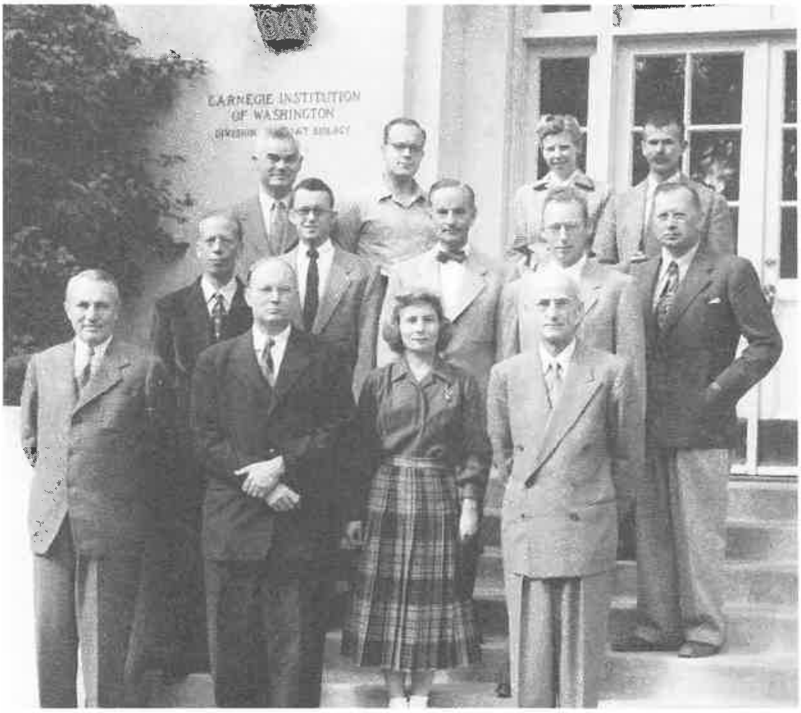
Like Spoehr, French got along well with Bush, with whom he shared a New Englander's talent as an inventor. From Bush's annual or semiannual visits, French came to admire the president's "intense interest in the details of our activities." Like others, French attested to the invigorating effect of Bush's mentality on others. The good relations continued after 1955 during the presidency of Caryl Haskins, who had first known French as a fellow graduate student at Harvard.

Investigations of photosynthesis became widespread in the United States and abroad during and after the 1950s, and the field became at times aggressively competitive. A large group at Berkeley and the Lawrence Radiation Laboratory were successful in working out the detailed cycle of carbon fixation (C_3) using radioactive carbon as tracer. The Carnegie investigators, unable to compete at that magnitude of effort, continued to seek forefront, but more manageable, questions, where contributions would advance the general and detailed understanding of photosynthesis.

Much of the work under French was in spectroscopic studies of photosynthetic pigments, especially the chlorophylls, and how they functioned in photosynthesis. In investigations stretching over several years, James Smith showed the formation of chlorophyll upon the illumination of an earlier-existing molecule called protochlorophyll. Smith and colleagues explored the transformation at various wavelengths and its response to changing factors—temperature, drying, substance infiltration. A major step was achieved in 1956 by research fellow Kazuo Shibata, who developed a method for recording absorption spectra of pigments in small amounts in living leaves, and applied it to the transformation of protochlorophyll to chlorophyll. The transformation previously could be studied only using killed leaves or by pigment extraction, but now absorption could be measured continuously throughout the process. An early result was the discovery of an intermediate chlorophyll form, previously unsuspected.

Among other important contributions was that of visiting investigator L. N. M. Duysens from the Netherlands, who in 1953 showed light-induced changes in absorption spectra in *Chlorella* and green plants, giving insights into carotenoid reactions. French, with visiting investigator Jack Myers, in 1958 explored the Emerson enhancement effect using two selected wavelengths alternately applied, thereby showing evidence for dark reactions, which proceeded even in the absence of illumination. In one of his several lines of investigation, David Fork (appointed staff member in 1961) worked with French using spectroscopic techniques to define how the two light reactions function in photosynthesis. Later Fork had an extended collaboration with Norio Murata, who visited regularly from Tokyo. Jeanette Brown came to the group in 1958, her laboratory skills complementing French's interests and, increasingly, leading her to independent work studying natural forms of chlorophyll and other pigments. Probably the topic closest to an overall focus of the group's recent work was in showing relationships of the different pigments, enzymes, and electron carriers in the electron transport chain, where captured photochemical energy is transformed to prepare for CO_2 fixation.

A distinctive strength of the photosynthesis group under French was in developing instrumentation and techniques for use in experiments. Excellent spectrophotometric instruments were not yet available commercially, so that primacy in discovery often went



October 1951. Front row (from left): H. A. Spoehr, C. S. French, Violet K. Young, W. A. Pestell. Middle row: H. W. Milner, E. A. Davis, J. H. C. Smith, Paul Grun, G. Clausen. Top: W. M. Hiesey, B. Kok, Jean Dedrick, M. A. Nobs.

to those investigators able to design and build the best instruments.

French, David Fork, and others at the Department thus built a succession of recording spectrophotometers and other instruments for various purposes, often well ahead of similar equipment used elsewhere. French himself, partly by personal inclination, spent much time in instrument design rather than in the conduct of experiments. (Vannevar Bush often contributed useful design ideas.) A prominent example was the French Press, where chloroplasts were extruded through a tiny needle valve, thus breaking them up and allowing their contents to be fractionated. The resulting chloroplast particles behaved chemically more like those in the whole plant than did particles obtained by detergent separation. The device remains today in wide use, at Carnegie and elsewhere, for breaking apart bacteria and other cells.

French, Fork, and the others had played a role well out of proportion to the group's size in building scientific understanding of photosynthesis. David Fork in late 1971 described some of the challenges that still remained—the evolution of oxygen in photosystem 2, the configuration of chloroplast membranes, the several competing theories explaining the synthesis of the final molecules needed for CO_2 reduction. Fork also described the importance of understanding the mechanisms whereby internal plant processes in photosynthesis are adapted to variations in environmental conditions, a topic that seemed to call for the combined strengths of the Department's photosynthesis and physiological ecology groups.

David Fork

The Outlook in 1972–1973

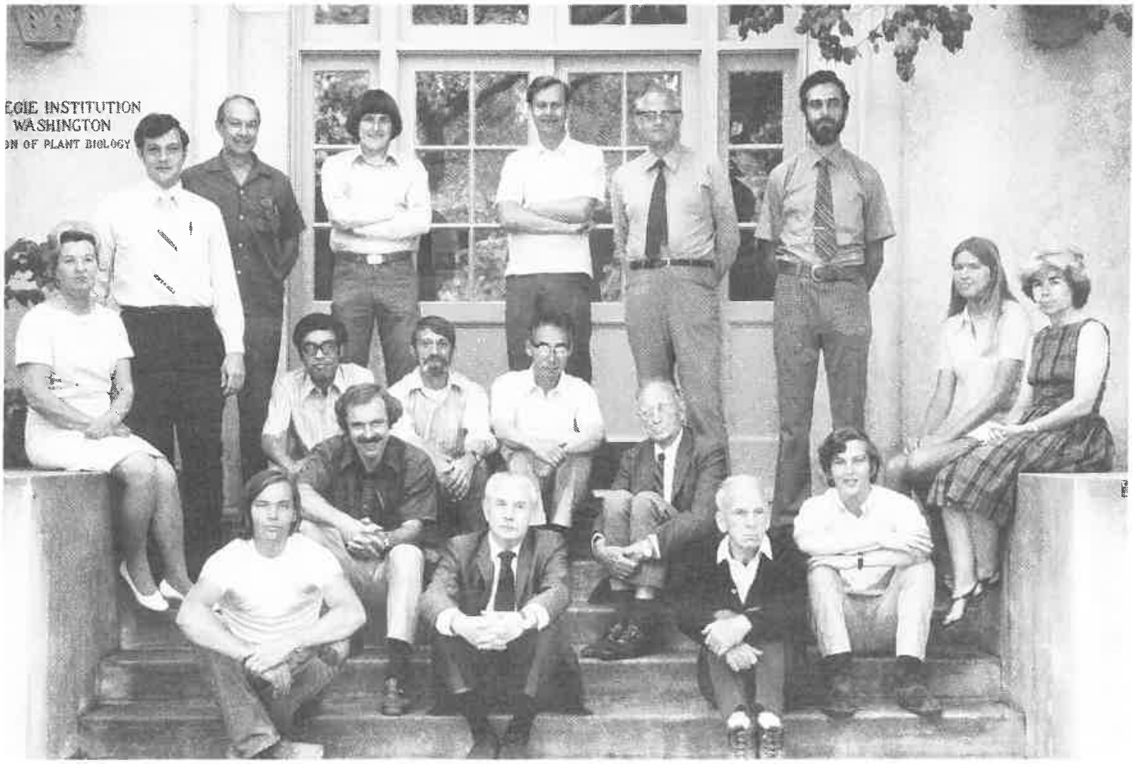
As French's retirement loomed in 1972, the auspices for the Department's future were not entirely encouraging. Whereas the plant biologists had in 1947 received about six percent of Carnegie Institution's annual budgetary appropriations, by 1972 the Department's share had declined to only a little over four percent. The figures plainly verified that the Department under French had made a virtue of frugality. But did they also indicate that the Institution's leaders had lost enthusiasm for investing in plant biology?

In actuality, such concerns among the plant biologists at Stanford were unwarranted. Philip Abelson, former director of Carnegie's Geophysical Laboratory and successor to Haskins as the Institution's president in 1971, formed a committee of five leading outside scientists to review the Institution's situation in plant biology and recommend a new director. Meeting at Stanford in June 1972, the members squarely endorsed the quality and significance of the Department's recent scientific work, especially in the study of photosynthesis.

> We want to emphasize that the Laboratory is a unique one in plant biology. In no other place are all the facets of photosynthesis so thoroughly and effectively addressed.

The committee also observed that although basic understanding of photosynthesis could be of critical importance for humankind, other groups were moving away from the subject. Indeed, the major funding program for plant biology administered under the government's National Institutes of Health had recently been closed.

As a successor to French, the committee members unanimously favored Winslow Briggs (b. 1928), then at Harvard, whose work in phototropism and photomorphogenic responses of plants suggested a common ground linking the Department's physiological ecology and photosynthesis groups.



Department of Plant Biology in 1972. Seated on steps from left: Ronald Atteberry, Tetsuo Hiyama, Frank Nicholson, David Fork, Jan Kowalik, Atusi Tahamiya, C. Stacy French, H. Lawrence, Tom Mathieson. Back row from left: Ruth Fischer, William Hager, Richard Hart, George Bowes, Olle Björkman, Hemming Virgin, Joseph Berry, Christine Shank, Jeanette Brown.

Briggs had earlier served for twelve years at Stanford University, and had collaborated with David Fork in several experiments at that time.

Briggs visited the Department for four days in November 1972, and afterwards gave Abelson several strong opinions as to what was needed. His prescription included the correction of the Department's "woefully deficient" equipment and facilities and the appointment of a "first-rate nucleic acid person." (French had been uninterested in the introduction of plant molecular biology, yet in its infancy.)

Abelson later confirmed that, in fact, no thought had been given to closing the Department. Nevertheless, the acceptance by Briggs of the directorship in 1973 set the stage for what became in several important respects a new beginning.

Reflections

Plant biology in 1973, indeed science itself, had vastly changed from early in the century. The Carnegie plant scientists, who had contributed in shaping the changes, had themselves adapted to a different role in science. Early in the century, they had been almost alone in studying plant ecology and photosynthesis; as late as the 1930s, their experimental taxonomy program represented a large-scale venture which few could match. But with the expansion of science in America after mid-century, the Department of Plant Biology, like the Institution itself, found itself a small fish in an ever-enlarging sea.

Thus the later Carnegie plant scientists sought manageable niches in which to contribute. The task was facilitated by their success in limiting themselves primarily to two major directions—photosynthesis and physiological ecology. Discernable in 1973 were stirrings that the two groups were growing together in interest and outlook. Meanwhile, befitting the increasing interdependence of scientists everywhere, the Department began an evolution toward becoming a kind of crossroads in the plant sciences—a place for collaboration with visiting investigators and talented postdoctoral fellows, individuals through whom the Department would fertilize new and rising areas of investigation worldwide.

* * *

Historians will probably long probe the chain of events leading to the closing of the Desert Laboratory in 1940. By this action, Carnegie forfeited not only a superb, long-protected site of over 800 acres but also the possibility of a future laboratory- and field-based desert studies program, perhaps like the one once proposed by Shreve which, arguably, might have provided a distinctive and pioneering niche well suited to the Institution's smaller place in science. Shreve's fine biographer, Janice Emily Bowers, understandably in sympathy with her subject, faults the Carnegie leaders for the decade-long starvation of activity at the Desert Laboratory in the 1930s and its final closure.

Unquestionably at play in these events had been Merriam's esteem for Spoehr and the modern kind of science represented by Spoehr's research. Spoehr's threatened resignation, it will be remembered, had lent impetus to the decision to build at Stanford. In contrast, Shreve quietly acquiesced in the scaling-down at Tucson. (Unlike Spoehr, Shreve had no equally suitable place to take his work.) Importantly, an "exceptional" successor to Shreve had neither appeared nor been developed.

Sentiment and polity aside, Merriam's reasoning, developed over many years, held compelling logic. Amid its serious fiscal troubles during and after the Great Depression, Carnegie Institution could not have supported a major program at Tucson without an equivalent termination elsewhere; in hindsight, things certainly worked out well at Stanford.

* * *

From the outset, Carnegie leaders and scientists expressed the view that fundamental research in plant biology would lead to important practical benefits for humankind. But by 1973, in a large sense, that expectation had not yet been fulfilled. The idea that an understanding of photosynthesis would lead to imitative ways of gathering and storing the energy of the Sun, for example, was still scarcely a realistic possibility. Moreover, projects seeking direct applications—the experimental program with *Poa*, for example, and the algal pilot plant—failed to produce the hoped-for benefits.

But the faith remained. Thus David Fork, in 1971, noted that it might become possible to manipulate photosynthetic intermediates to influence the products in food plants, perhaps enriching them in protein or fats, for example. Perhaps one day, Fork wrote, knowledge of photosynthesis might enable humankind to synthesize organic matter from inorganic materials.

* * *

This historian may be allowed to dwell for a moment on that hardy band of young men and women who came early in the century to study the desert—Cannon, MacDougal, the Shreves, Spoehr, indeed the Clementses. Tracking the careers of these heroes into old age has been a moving experience. Their curiosity, their respect for nature, their lifetime commitment to its understanding, were captured in words once written of Forrest Shreve by his friends:

> He became almost a part of the desert he studied and knew so well.

Author's note:

This history is based primarily on materials in the archival files of the Carnegie Institution and on published writings by the subject scientists, mainly in the Year Books and other volumes published by the Institution. There is also reliance on material by other authors, including Janice Emily Bowers, Robert P. McIntosh, F. E. Egler, Sharon Kingsland, Peter Dreyer, Joel B. Hagen, William Maginnies, Judith C. Wilder, and Franklin Portugal. Although I believe that the interpretations offered here are sound, a definitive account would require research in other archival collections. The story plainly merits a fuller monograph or book.

Readers of this essay in manuscript form were Winslow Briggs, Maxine Singer, David Fork, C. Stacy French, Olle Björkman, William Hiesey, Malcolm Nobs, Patricia Craig, John Lively, and Linda Feinberg. Assistance was also given by Susan Fraser of the New York Botanical Garden, Deborah Shelton of the Arizona Historical Society, Sharon Kingsland of the Johns Hopkins University, and Philip Abelson, former president of the Carnegie Institution. The help and encouragement of all these individuals is appreciated, but responsibility for any remaining errors or misrepresentations remains mine.

—Ray Bowers
Editor, C.I.W.
December 1991

Some additional reading:

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